BOTANICAL GAZETTE

JANUARY 1911

THE ORIGIN AND TAXONOMIC VALUE OF THE "VEIL" IN DICTYOPHORA AND ITHYPHALLUS[1]

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(WITH PLATES I–VII AND ONE FIGURE)

Although *Ithyphallus impudicus* is quite common and widely distributed in Europe, a complete and satisfactory account of its development, which is sufficient for a full comparison with other related plants, has not yet been given. This is probably due to the fact that it is very difficult to find a sufficiently large number of good specimens in the young stages of development. The more recent and most nearly complete accounts are those by ED. FISCHER (**6**, p. 22; **7**, p. 12) and VAN BAMBEKE (**17–21**). The gross structures in the later stages of development had already been described by ROSSMAN (**14**, p. 185) and by DEBARY (**3**, p. 203), but FISCHER studied the principal features in the origin and development of the parts within the undifferentiated fruit bodies, from the time when they first make their appearance on the rhizomorphs as minute undifferentiated structures, only a few millimeters in diameter, up to their complete differentiation.

Notwithstanding the valuable results which are presented in these contributions, there still remain some questions concerning which there is a difference of statement and opinion as expressed by several students and writers on the Phallales. These questions relate to the very early origin and differentiation of the fruit body,

[1] Contribution from the Department of Botany of Cornell University, no. 138.

NOTE.—Investigation prosecuted with the aid of a grant from the Botanical Society of America in 1905.

and especially to the origin and homology of the so-called "veil," which is described in some species but is often regarded as absent in others. For example, a rather persistent membranous "veil" is described in *Phallus ravenelii* B. and C., an evanescent membranous veil in *Ithyphallus tenuis* Ed. Fischer (PENZIG **13**, p. 146), while *Ithyphallus impudicus* is often regarded as wholly lacking a veil at the time of the expansion of the plant.

This study was undertaken with the purpose of answering, if possible, some of these questions. It naturally led to a study of the origin of the veil in *Ithyphallus impudicus*, and to a comparative study of this structure in *I. impudicus* with the "veil" in *Phallus ravenelii* B. and C., and the "indusium" in *Dictyophora duplicata* (Bosc.) Ed. Fischer; and to a consideration of the generic value of these structures.

While studying and photographing the fungi of France in the vicinity of Pontarlier, France, and other villages in that section of the Jura Mountains, I had an opportunity of collecting considerable material of *Ithyphallus impudicus* in different stages of development. Several individuals were first found and collected by my friend M. A. COURTET,[2] who accompanied me on many of the excursions, and showed me the locality where this plant was growing. It was in a forest by the roadside, and the plants were growing for some distance around an old decaying stump. In the vicinity of some of the rotten wood, strands of the mycelium were found with numerous very young fruit bodies. Others were found which were older, thus presenting an interesting series of development from the very young and minute fruit bodies to the mature plants (text fig. 1). As many as possible of these were collected in different stages. Not having any other fixer at hand, they were fixed in alcohol and picric acid, and then preserved in 75 per cent alcohol.

In the very early stages of the development of the young fruit bodies, their structure corresponds very closely with that of the growing end of the rhizomorphs as described by DEBARY (**3**, p.

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203), and later by FISCHER (**6**, p. 23). These rhizomorphs consist of a central strand or core, and a cortex. The central strand or core is composed of hyphae, the general direction of which is parallel with the axis, while here and there certain hyphae turn outward with the cortex. Between the hyphae there is more or less gelatinous substance, which is more abundant in the central portion of the core, where the threads are rather distant, while on its periphery they are more crowded. These threads stain readily, so that

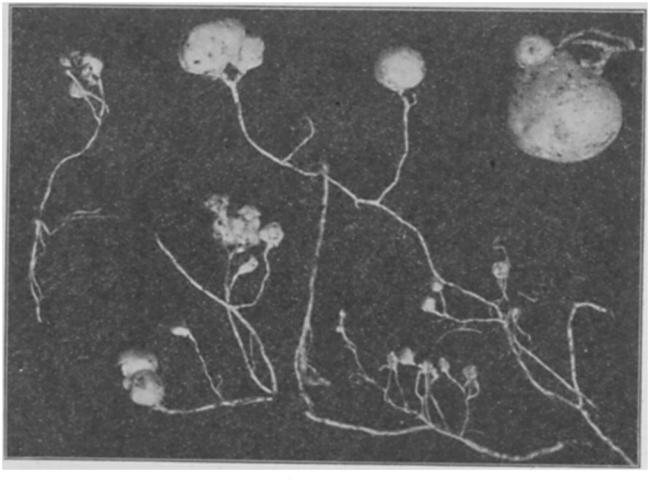

FIG. 1.—Rhizomorphs and young fruit bodies of *Ithyphallus impudicus*, from Pontarlier, France, 1905; natural size.

in longitudinal sections this medulla or core stands out distinctly from the rather thin cortex.

In the young fruit bodies, according to FISCHER (**6**, p. 23), this medulla is present and terminates in a tissue of slender hyphae which are rich in protoplasmic content. This central portion of the pyriform young fruit body has the form of a sheaf, which in longitudinal section presents a fan-shaped outline. This tissue also stains readily and is surrounded by a cortical layer of looser texture, the external portion of which contains hyphae and crystals of calcium oxalate, exactly like those in the cortex of the rhizomorphs. BURT (**1***a*, p. 347) describes a similar structure in the young fruit bodies of *Mutinus caninus* (Huds.) Fr., but differs from

FISCHER in regard to the part which the central core or medulla plays in the formation of the mature fruit body. According to FISCHER, the wall of the "stipe" (the stemlike portion of the receptacle) is formed on the outside of the portion of the medulla which lies within the young fruit body, so that this portion of the medulla or central strand would lie within the stipe. According to BURT, in *Mutinus caninus* the central strand, while connected with the central mass of tissue in the young fruit body, does not take part in the formation of the stipe. All parts of the fruit body, with the exception of the external portion of the outer layer of the volva, are, according to him, derived from the deeply staining mass of tissue which lies in the center of the broadened end of the young fruit body. The examination which I have been able to make of longitudinal sections of young fruit bodies of *Ithyphallus impudicus*, in the different stages of development, leads me to believe that the position and extent of development of this central strand in the young fruit bodies is a variable one.

In the center of the broadened end of the very young fruit body there arises a homogeneous, compact tissue, composed of intricately interwoven hyphae rich in protoplasm. This tissue may be regarded as fundamental or primordial tissue, which later gives rise by growth and differentiation to the parts of the mature plant. In none of the very young fruit bodies, just prior to or at the time of the appearance of this central primordium, of which I succeeded in getting longitudinal sections, was there a direct continuation of the central strand into the middle portion. The hyphae of the central strand, singly or in fascicles often fan-shaped, diverge in various directions and seem to be lost near the periphery of the proximal end. The central portion of the young fruit body is probably developed from the young apical region of the central strand, but in none examined have I seen the strand as a whole in connection with the central primordium, or, as already stated, even extending into the central region of the young fruit body. My sections have been studied very carefully in this respect, since BURT in *Mutinus caninus* and FISCHER in *Ithyphallus impudicus* have found the strands as a whole extending into the interior of the fruit body, and as a whole in connection with the central

primordium. The failure to find it in this connection in the specimens examined by me is not to be taken to mean that in some or in many specimens it is not so connected with the central primordium, but rather lends support to the view held by BURT that the medulla of the rhizomorph, when it does extend into the center of the young fruit body, is not concerned in the organization of the members of the mature plant, but that these are organized from the central primordium.

The first evidence of the differentiation of the primordium is the gelatinization of the hyphae in the extreme upper portion just inside the cortical layer. This occurs in a small circular area which progresses centrifugally and downward from its edge, so that it becomes at first convex (fig. 17), and later campanulate, as it extends downward on all sides in the area, occupying the same relation to the central primordium and cortex. This forms the thick gelatinous middle layer of the volva. In the early stages of this gelatinous area, the swelling of the gelatinous substance, formed from the outer layers of the hyphae, crowds the hyphae apart and they form an irregular open network with large, more or less rounded gelatinous masses in the mesh. But with the formation of more of the gelatinous substance and the broadening of this layer, many of the hyphae are stretched in a radial direction, extending from the tissue which later forms the inner layer of the peridium (figs. 19–22).

While the development of this gelatinous layer is progressing, and soon after its inception, the fundaments of other parts begin to make their appearance. The fundament of the stem appears in longitudinal section (figs. 18, 19) as a delicate columnar structure. The central portion of this structure consists of primordial or fundamental tissue, which is but little colored by the stain, while the fundament of its wall stains deeply and extends nearly up to the apex of the bell-shaped structure inside of the gelatinous layer. The bell-shaped area adjacent to the inner surface of the gelatinous layer, which takes a deep stain, is to form the inner wall of the peridium (*D*, figs. 19, 21). Lying directly next to this on the inner side is the fundament of the gleba (*G*, fig. 19), also a bell-shaped area, but not yet differentiated from the former.

Farther within (*P*, fig. 19) is another bell-shaped area which takes a deeper stain than the fundamental tissue on either side. This is the fundament of the inner portion of the pileus.

The remaining primordial tissue lying between the fundament of the pileus and that of the stipe is in the form of a hollow cone, the wall of which is broad at its base. It is the tissue which DEBARY (**3**, p. 204) called the cone (*Kegel*). In the stained section, a photograph of which is represented in figs. 18, 19, this cone of primordial tissue does not show a homogeneous structure. At *I* there is a deeply stained area, also campanulate in form when taken as a whole, lying within the lighter colored portion of the cone. This is what I regard as the fundament of a true indusium, which in *Ithyphallus impudicus* does not become further differentiated, so far as present evidence indicates, though the rudiment may persist in a recognizable form (in magnified section) up to the maturity of the plant. The hyphae here are somewhat more densely interwoven, and therefore this zone stains more deeply in contrast with the other primordial tissue on either side of it. This rudiment of an indusium described by FISCHER (**6**, p. 26) remains in the condition of primordial tissue, which, with some adjacent primordial tissue, in the mature plant forms a thin membrane lying between the pileus and the stipe. My interpretation of the fundaments represented by these more deeply staining cones in the young fruit body of *Ithyphallus impudicus* is slightly different from the interpretation given by FISCHER. The zones in fig. 19 indicated by *P* (pileus fundament), *I* (indusium fundament), and *B* (primordial tissue lying between) are considered by FISCHER as one zone, the fundament of an indusium which he marks in his figures as *I*. An examination of his figures shows that it is made up of three layers or zones, two outer ones more deeply stained than the inner one, corresponding to the three zones of my figure (*P*, *B*, and *I*). FISCHER states that the outer layer of his zone *I* forms the inner layer of the pileus, and that the indusium in *Dictyophora phalloidea* Desvaux is differentiated along the inner layer of the zone *I*. Zone *I* of my figure joins the stem at the same place as the inner layer of FISCHER'S zone *I*, and also in the mature fruit body, as will be shown later, the zone *I* of my

figures can be distinguished as a more deeply staining layer within the thin membrane of primordial tissue lying between the stipe and pileus, joining the stipe at the projecting ring of the same near the apex of the stipe at the corresponding point where the indusium of *Dictyophora duplicata* joins the stem. These facts lead me to believe that the fundaments represented by the more deeply staining zone in the young fruit body should be interpreted in accordance with their treatment here.

Another peculiar structure sometimes appears at this stage. It lies in the lighter colored zone (figs. 19, 20), and in stained longitudinal sections appears as a delicate line, deeply stained, lying some distance from the fundament of the stem wall, but diverging from it and not presenting the curved contour of the other zones. The walls of the hyphae appear to be slightly gelatinized or thickened and take the stain deeply. Perhaps it represents the beginning of a partial degeneration of the fundamental tissue which does not take part in the formation of any of the members of the plant. Or it may represent a very slight tendency to the formation of the pseudoparenchymatous tissue of an indusium such as exists in a well developed form in *Dictyophora*, since this structure lies close to the fundament of the indusium.

The fundament of the gleba now gives rise upon its inner face to a palisade layer of slender clavate cells. This layer, as it progresses, develops unevenly, forming numerous folds, with furrows between them, which branch profusely as they extend inward toward the forming pileus. Figs. 19 and 21 are from a section, nearly longitudinal, which shows the partially developed members of the plant; *D* is the inner peridium of the volva, *G* is the developing gleba, *P* is the forming pileus, *A* is the apex of the stipe, while *I* is the fundamental tissue between the stipe and pileus. At maturity this fundamental tissue lies between the stem and pileus as a thin, delicate, membranous layer, which also extends below the pileus around the lower end of the stipe. This is undifferentiated tissue. As the stem elongates and the pileus expands somewhat, this delicate membrane or "veil" is torn and fragments are left on the surface of the stem, and occasionally some of them on the inner surface or margin of the pileus. These fragments often

lie around the stem a short distance below the margin of the pileus in the form of a ring (fig. 1). It is so delicate that it collapses, dries, and disappears very soon after the expansion of the plant, or is washed away by the rains, so that it is probably rarely seen except by those who collect the mature "eggs," and in a protected place observe the unfolding of the plant.

The delicate and evanescent character of this "veil" may account for the fact that it is rarely shown in connection with illustrations of this species after expansion, especially in works of a general character. This has probably led to the rather widespread belief, especially in some quarters, that a "veil" is wanting in *Ithyphallus impudicus*. The variability in the strength of this "veil" in individuals of the same species, and in different species, as well as the presence of the indusium in *Dictyophora*, occupying a similar position between the pileus and stem, though of a different structure and ontogenetic history, has led to considerable confusion regarding its nature, origin, and taxonomic value. Many writers have used the terms "veil" and "indusium" synonymously. If the word *velum* or "veil" were used to designate the remnant of primordial or fundamental tissue lying at maturity of the plant between the pileus and stem, and if the word *indusium* were reserved for the organ of different structure which is differentiated and developed from a portion of and within this primordial tissue, it should serve to clear away the existing confusion. A comparison of these structures and a consideration of their origin and later history in *Ithyphallus impudicus*, *Dictyophora duplicata*, and *Phallus ravenelii*, with photographs of stained sections, together with a discussion of some of the literature of the subject, it is hoped will lead to a more intelligent understanding of their nature and taxonomic significance than can be obtained from an examination of them at the time of the expansion of the plants.

Ithyphallus impudicus is a rare plant in the northeastern part of the United States. I have never seen a specimen from this region. *Dictyophora duplicata* is rather common, however. Its size and form, as well as the surface of its pileus, are so similar to *I. impudicus* that, as BURT (1*b*, p. 384) remarks, there is danger

of mistaking the two in the younger stages, while the indusium remains adherent to the under surface of the pileus before the intervening primordial tissue is ruptured. In old plants after expansion, when the indusium has fallen away, as frequently happens, there is danger of confusing it with *I. impudicus*. *Phallus ravenelii* is also sometimes mistaken for *I. impudicus*, but this should not happen when one is familiar with the character of the pileus in the two species, and with the very different odors of the two.

The first time that I met with growing examples of *Ithyphallus impudicus* was in September 1903, when in company with Mr. GEORGE MASSEE I found two mature eggs in the Kew Gardens. These were taken to the Jodrell Laboratory and placed under a moist chamber. During the night one of them expanded, and on the following day there was very clear evidence of a thin, white, membranous veil between the stem and pileus, which was now lying on the stem a short distance below the pileus and partly encircling the stem as a ring. I photographed the plant at the time, and the presence of this veil is very distinctly shown as a complete membranous ring around the stem (figs. 1, 2). The plant was then placed in alcohol, shipped by freight to this country along with other fungi, and it is now stored in alcohol in a museum jar in the Department of Botany in Cornell University, and shows well at the present time this thin, membranous veil.

In August 1905, in the Jura Mountains at Pontarlier, France, I reared several plants in moist chambers from mature eggs. In all of these the veil was present and adhered either as fragments or as a ring on the stipe. Sometimes also fragments clung to the margin or under surface of the pileus. Several photographs were made of these and one is shown in fig. 2. It is interesting to note in this photographic reproduction the collar around the stipe below, which is the lower remains of the veil where it is attached to the broader remnant of primordial tissue. This is exactly the same structure that is present at this stage in *Phallus ravenelii*. Dissection of the eggs can be made also in such a way as to show a distinct, thin, membranous veil between the stem and pileus before expansion (fig. 8). The veil thus separated from the two

adjacent surfaces of contact stands out clearly, and is continuous from its attachment with the primordial tissue at the base of the stem and volva below to the apex of the stem at the point where the latter joins the pileus.

While, as previously stated, there is quite a widespread belief that a veil is wanting in *I. impudicus*, there is abundant evidence that it was observed by the earlier students of these plants. CORDA (**2**) figured and described it as early as 1842. His figs. 1, 2, and 3 show a thin veil. He calls it outer stem veil (*äussern Strunkeschleier*[3]). DEBARY (**3**, p. 207) speaks of it as a thin, white membrane between the pileus and stem, which is torn into fragments as the stem elongates. His language[4] shows that various authors spoke of it as a veil (velum), and he himself uses the term after the expansion of the plant, when fragments of it cling to the stem. KALCHBRENNER (**8***a*, p. 63) describes and figures it as present in *Phallus imperialis* Schulzer, which is but a form of *I. impudicus* (see ED. FISCHER **6**, p. 84). FISCHER (**6**, p. 27) describes it as a hyphal weft between the stem and pileus in the mature egg. He regards it as a remnant of the primordial tissue, but does not speak of its appearance after the expansion of the plant. BURT (**1***b*, p. 384) says that the veil is wanting in *I. impudicus*. In his characterization of the genus *Ithyphallus* he says "veil wanting." By this he probably means that a persistent, entire veil, such as is usually present in *Phallus ravenelii*, is wanting in the genus *Ithyphallus* as interpreted by him.

In *Phallus ravenelii* the veil is usually persistent, is composed of a thicker hyphal weft of primordial tissue, and is therefore not so easily torn into fragments, but persists as a campanulate, membranous collar suspended around the stem under the pileus from

[3] "Im geschlossenen Eie zwischen dem Hute und dem Strunke eine feine, weisse, zarte Haut, emporschicht, welche den äussern Strunkeschleier (fig. 1[1]) bildet, welche bei Verlangerung des Trägers zum Steile, zerreisst, und dessen zarte Fragmente bald verschwinden."—*Icones* 5:71–73. *pl.* 7. *figs.* 1–3. 1842.

[4] "Sie erhält zuletzt die Gestalt einer dünnen weichen Haut welche von den Autoren der Schleier (velum) des Stiels genannt worden ist. . . . . Der Kegel reisst in seinem untersten Theile quer durch; die mit dem Basalstücke zusammenhängende Portion bleibt mit letzterm als eine die Stielbasis umgebende napfförmige Scheide stehen; der obere Theil zerreisst in unregelmässige Fetzeln, welche theils zwischen Hut und Stiel, theils auf der freien Aussenfläche des letzteren hängen bleiben (velum)."

the point of their junction. For this reason it is apt to be overlooked unless one is careful to look between the pileus and stem, or unless a section of this part of the plant is made. Sometimes the veil is torn into a few fragments, and at other times it may become free from its point of attachment and lie as a ring or band of membranous tissue around the stem below the pileus. It is then quite plainly seen. This is shown in the photograph reproduced in fig. 5. This figure also shows the membranous collar around the base of the stem with which the veil was connected before expansion of the plant, when it was torn apart.

In the first published description of *Phallus ravenelii* B. and C. (**1**, p. 33) no mention was made of the presence of this veil. FARLOW (**4**, p. 247) describes it and speaks of it as a rudiment of a veil. PECK (**12**, p. 123) also describes and figures it. He speaks of it as an indusium or veil, and states that RAVENEL, on whose notes and specimens BERKELEY described the plant, had made a complete description of this veil in his notes, which BERKELEY failed to include in his description. MORGAN (**11**, p. 146) places *P. ravenelii* in *Hymenophallus* (as a subgenus of *Phallus*) along with *P. duplicata* Bosc. (*Dictyophora duplicata*), thus considering it more closely related to the present *Dictyophora* than to *I. impudicus*, which he places in *Ithyphallus* (as a subgenus of *Phallus*). In this respect he followed GERARD (**8**, p. 11). He speaks of the veil as an indusium or veil which is reticulate in some species of *Hymenophallus*, and not reticulate in others, and is dependent from the apex of the stem underneath the pileus. In *Ithyphallus impudicus* he recognizes the thin membrane between the pileus and the stem which is torn into shreds as the plant expands.

ED. FISCHER (**6**, p. 30) placed *P. ravenelii* in the genus *Ithyphallus* because he believed a true indusium, homologous with the indusium of *Dictyophora*, was absent. In the study of a few young fruit bodies he finds (**7**, p. 16) not only no evidence of a true indusium in the primordial tissue between the stem and pileus, but also no evidence of a fundament or the beginning of a differentiation of tissue which would indicate a rudimentary indusium. BURT (**1***b*, p. 385) regards the veil in *P. ravenelii* as homologous with the indusium of *Dictyophora*, probably being influenced more by

its usual persistence as a distinct membrane than by its ontogenetic history, though he states (1*b*, p. 386) that some laterally inflated toward hyphae led him to believe that this indicates a differentiation pseudoparenchymatous tissue. SCOFIELD (**15**, p. 533) does not consider the veil in *P. ravenelii* to be a differentiated organic structure, but a remnant of the tissues of the young fruit body. Consequently he follows FISCHER in placing the species in the genus *Ithyphallus*. It appears that LLOYD (**9**, p. 327) treats the indusium of *Dictyophora* and the veil of *Ithyphallus*, even the very thin and fragile veil of *I. impudicus*, as homologous structures, probably without a consideration of their different origin and ontogenetic history, since he thinks "the only difference is in the degree of development of the veil." On this basis he would discard the genus *Dictyophora*, and place all three of the species in question here in the genus *Phallus*.

There are two methods by which the relative value of these structures (the "veil" and indusium) in showing generic relationship may be considered: (1) by their morphology, that is, their form, structure, and position relative to other organs of the plants; and (2) by their origin and differentiation in the individuals, or in other words their ontogenetic history. According to the first, it is not sufficient that we should compare these structures after the expansion of the plant. Some of the present confusion probably can be traced to observations made only at this stage of development. Observations and comparisons should also be made before the elongation of the stipe has so disarranged the parts as to make impossible a careful comparative study of these structures in their normal position. For the purpose of this study fruit bodies of the three species (*I. impudicus*, *P. ravenelii*, and *D. duplicata*) were selected a short time before complete maturity, but after complete differentiation of the parts had taken place, and only a comparatively short time before the period of elongation. Microtome sections were made of these, longitudinally at the upper and lower ends of the "egg," and transversely as well as longitudinally in the middle region. These sections included the volva, pileus, and one side of the stipe (to or near the middle), and of course the tissues in question between the pileus and stipe, and the base of

the volva. These were stained, mounted in balsam, and then photographed at various magnifications, as indicated in the description of the plates. They were also subjected to careful microscopic study.

It will be interesting to study the figures here reproduced from some of these photographs. Figs. 9, 10, 11 are from longitudinal (radial) sections at the base of these three species. Fig. 9 is *Ithyphallus impudicus*, and the parts are as follows (the outer layer of the volva is not shown here): *F*, gelatinous layer of the volva; *D*, inner layer of the volva; *G*, gleba; *P*, pileus; *A*, stem; *B*, primordial tissue. The primordial tissue shows no differentiation. It consists of intricately interwoven hyphae and is a remnant of the primordial tissue of the young fruit body, which has been left behind after the organization of the other parts of the plant. Next the pileus and the stipe there is a slightly darker line, the result probably of a slight massing or distintegration of those hyphae which are crowded by the enlarging stem and pileus. There is no evidence here of the differentiation of another structure within this primordial tissue. At the narrowed portion above is the point near which the primordial tissue is torn apart in the elongation of the stem, separating the thin, membranous part from the broader part below (see fig. 2).

Fig. 10 is of *Phallus ravenelii*. The primordial tissue lying between the base of the stem and the lower part of the pileus also shows no differentiation, the portions next the pileus and stem staining slightly darker, as in *I. impudicus*, and from the same cause. This represents a rather thin veil for *P. ravenelii*, and therefore serves to show, aside from there being no difference in its structure, position, and relation at this point in the fruit body from the veil of *I. impudicus*, that it is not any more massive. A short distance above the margin of the pileus is the point where the veil ruptures, leaving the collar of primordial tissue around the base of the stem as in *I. impudicus*.

Fig. 11 is of *Dictyophora duplicata*. The parts are lettered as in the two previous figures of *I. impudicus* and *P. ravenelii*. We note outer layer of volva; *F*, gelatinous layer of volva; *D*, inner layer of volva; *G*, gleba; *P*, pileus; *A*, stem; and *B*, primordial

tissue. There is here, however, an additional organ, or part of the fruit body, which lies within the primordial tissue, leaving a thin layer of primordial tissue next to the stem and one next the pileus. This is the indusium (*I*), which in this species is composed of chambered, pseudoparenchymatous tissue differentiated from and within the primordial tissue and not extending down into the tissue at the base. The remnant of primordial tissue here is exactly homologous with that which we have just observed in *I. impudicus* and *P. ravenelii*. In this figure there is seen the thin, white membrane or veil which lies between the indusium and the stem, and which is continuous with the more massive area of primordial tissue below. The remnant of primordial tissue between the pileus and indusium is in this specimen, at this point, very thin, but it is present and can be seen extending around below the margin of the indusium to join the other branch where the two veils or membranes pass into the mass of primordial tissue below.

Fig. 12 is of a longitudinal section from *I. impudicus* at the upper end of the fruit body, the lettering as before. Here we should note the inner and outer layers of the main part of the pileus, which in the section stain as dark lines in contrast to the looser tissue of the trama between. The inner wall of the pileus can be here traced upward as a very distinct dark line. For want of space, the entire photograph is not reproduced here, the upper portion being cut away; but the pileus above curves over and is joined with the margin of the stem apex. Between the pileus and the stem is seen the primordial tissue, the "veil." A very interesting structure is present here. Through the middle of the primordial tissue, parallel with the surface of the pileus and stem, but separated from them on either side by primordial tissue, is a darker line, represented by slightly denser tissue which stains darker than that on either side. This is the indusium rudiment described earlier in the study of the development of the young fruit bodies, and it is quite remarkable that this rudiment should persist within the veil up to the maturity of the fruit body, so that it can be recognized in microscopical preparations. It does not continue to the apex of the stem along with the membrane of primordial tissue, but ends a short distance below at the projecting ring in the stem correspond-

ing to the point where it was observed in the younger fruit bodies, and also to the point where the well organized indusium of *Dictyophora* is attached (see fig. 13).

Fig. 13 is from a similar section of *D. duplicata*, that is, a longitudinal section at the upper part of the fruit body; the indusium (*I*) is joined to the stipe at the point where the annular projection occurs. The main portion of the remnant of primordial tissue lies between the indusium and stipe, a very thin layer only lying between the indusium and pileus, which is continuous with the primordial tissue above the indusium between the stipe and pileus. The dark line at the edge of the primordial tissue next the indusium is caused by the denser accumulation of hyphae as they have withdrawn or have been pushed back by the folding and crowding of the chamber walls of the indusium. In this figure can be seen also the delicate weft of hyphae lying in the chambers of the stipe, pileus, and indusium. This is the remnant of primordial tissue within and from which these parts were organized. It is continuous at certain points with the "veil" or membrane of primordial tissue lying between the stipe and pileus and enveloping the indusium. A similar weft of primordial tissue lies within the chambers of the stipe and pileus in the other species.

Fig. 14 is from a longitudinal section in the same region of the fruit body of *Phallus ravenelii*. The "veil" (*B*) is seen to consist of undifferentiated tissue, that is of primordial tissue. There is no evidence of a distinct organ like the indusium of *Dictyophora* lying within it, nor even of a fundament or rudiment of such an organ. The primordial tissue is a homogeneous weft which is continuous between the chambered walls of the stipe.

It will be interesting now to examine cross-sections near the middle region of the fruit body at the same stage of development. *Phallus ravenelii* presents nothing essentially different from that shown in fig. 14; but from a comparison of the photographs of these sections from *Ithyphallus impudicus* (fig. 15) and *Dictyophora duplicata* (fig. 16), the impression is at once gained that in *Dictyophora duplicata*, as represented by this specimen, there is a "veil," in addition to the indusium, quite as strong as that present in *Ithyphallus impudicus*. It is therefore quite possible that, at the

time of expansion of the plant, fragments of a veil are to be found in addition to the well developed indusium. In some examples of *Phallus ravenelii* the "veil" is scarcely more massive than is here represented in *Dictyophora duplicata*. The fact that in *Phallus ravenelii* it is usually more massive and thus more permanent, is not a sufficient ground for considering it homologous with an entirely different organ in other species, which originates within and from a portion of this primordial tissue.

The corresponding cross-section of *Ithyphallus impudicus*, reproduced in fig. 15 from a photograph, is very instructive in this connection. Lying within the primordial tissue and parallel with the surfaces of the stipe and pileus wall is a thin layer of more deeply staining tissue. This is the fundament or rudiment of an indusium, which was observed in the longitudinal section of the upper part of the fruit body, and first appears in the young fruit body at the time of the origin of the fundament of the pileus. It has not advanced beyond the condition of primordial tissue, but the more dense arrangement of the hyphae and their deeper staining reaction is retained, in some examples at least, up to the maturity of the fruit body. As already stated, ED. FISCHER has described and figured the fundament of the indusium in the very young stages of *Ithyphallus impudicus*, although I differ slightly from him as to the limits of this fundament. It is homologous with the corresponding stages of the indusium fundament in *Dictyophora phalloidea* as described and figured by him. In the young stages of *Phallus ravenelii* studied by him (**7**, p. 15) he found no evidence of even a fundament of the indusium, though the material which he studied did not include the very young stages.

From all that has been determined in connection with this study, however, together with the results of other investigations on these species, the conclusion that a true indusium is wanting in *Phallus ravenelii* appears to be justified. If *Dictyophora* is to be retained as a genus distinct from *Ithyphallus*, as at present I believe it should be, *Phallus ravenelii* cannot properly be placed in the genus *Dictyophora* if the indusium of this genus is to be interpreted in the light of its ontogenetic history and distinct differentiation from primordial tissue, rather than upon the mere fact of the

presence of a campanulate structure more or less persistent and usually but not always suspended between the pileus and stipe, without regard to the important question of its real homology. With regard to the generic position of *Ithyphallus impudicus* the question may arise as to whether or not it should be placed in the genus *Dictyophora* on account of the rudiment of an indusium within the primordial tissue. If a rudimentary condition of an organ were to have the same taxonomic value as the well developed condition of the same organ, *I. impudicus* would be congeneric with the species of *Dictyophora*. But a rudimentary condition of an organ is not generally regarded as of equal taxonomic value with its well developed state in other species, though it may be of value in a study of phylogenetic relationship. *I. impudicus*, therefore, should not be placed in *Dictyophora*, or rather is not congeneric with it, though, curiously, it probably shows a closer phylogenetic relationship to that genus than does *Phallus ravenelii*. *Phallus ravenelli* B. and C. and *Ithyphallus impudicus* (L.) are then to be regarded as congeneric, and if the genus *Ithyphallus* is to be retained, the former should then be known as *Ithyphallus ravenelii* (B. and C.) Ed. Fischer.

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DESCRIPTION OF PLATES I–VII

Magnifications are as follows: figs. 9–13, 18, 22, ×10; figs. 14–17, ×25. Photographs by the author.

PLATE I

FIGS. 1, 3.—*Ithyphallus impudicus* from Kew Gardens, England, 1903; fig. 1 enlarged from kodak fig. 3.

FIG. 2.—*Ithyphallus impudicus* from Jura Mountains, France, 1905, showing "veil" around stem below pileus; at the base showing the collar of fundamental tissue which was ruptured on expansion of plant.

PLATE II

FIG. 4.—*Phallus ravenelii* from Ithaca, N.Y., showing "veil" around stem below pileus; at base showing the collar of fundamental tissue as in *Ithyphallus impudicus*.

FIG. 5.—Same with pileus cut away from the front to show upper part of "veil" suspended from apex of stem underneath pileus; two rings of this "veil" of fundamental tissue below on the stem; at base collar of fundamental tissue.

PLATE III

FIG. 6.—*Dictyophora duplicata*, Ithaca, N.Y., showing indusium.

FIG. 7.—Dissection of egg of *Phallus ravenelii*, showing continuous veil of primordial tissue between pileus and stem.

FIG. 8.—Similar dissection of *Ithyphallus impudicus*, showing continuous veil of primordial tissue between pileus and stem.

PLATE IV

FIG. 9.—Longitudinal radial section at base of egg of *Ithyphallus impudicus: A*, stem; *B*, primordial tissue which forms the collar; *P*, inner portion of pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

FIG. 10.—Longitudinal radial section at base of egg of *Phallus ravenelii: A*, stem; *B*, fundamental tissue which forms the collar; *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

FIG. 11.—Longitudinal radial section at base of egg of *Dictyophora duplicata: A*, stem; *B*, fundamental tissue which forms the collar and extends upward as a thin veil on either side of *I* (indusium); P, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE V

FIG. 12.—Longitudinal radial section through upper part of egg of *Ithyphallus impudicus: A*, stem; *BB*, fundamental tissue with rudimentary indusium; *I*, indusium lying with it; *P*, pileus; *G*, gleba; *D*, inner peridium.

FIG. 13.—Longitudinal radial section at upper part of egg of *Dictyophora duplicata: A*, stem; *BB*, fundamental tissue; *I*, indusium; *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE VI

FIG. 14.—Longitudinal radial section through upper part of egg of *Phallus ravenelii: A*, stem; *B*, fundamental tissue; *P*, pileus; *G*, gleba.

FIG. 15.—Transverse section through middle part of egg of *Ithyphallus impudicus: A*, stem; *B*, fundamental tissue; *I*, rudiment of indusium within it; *G*, gleba; fundamental tissue also lies between *I* and *P*.

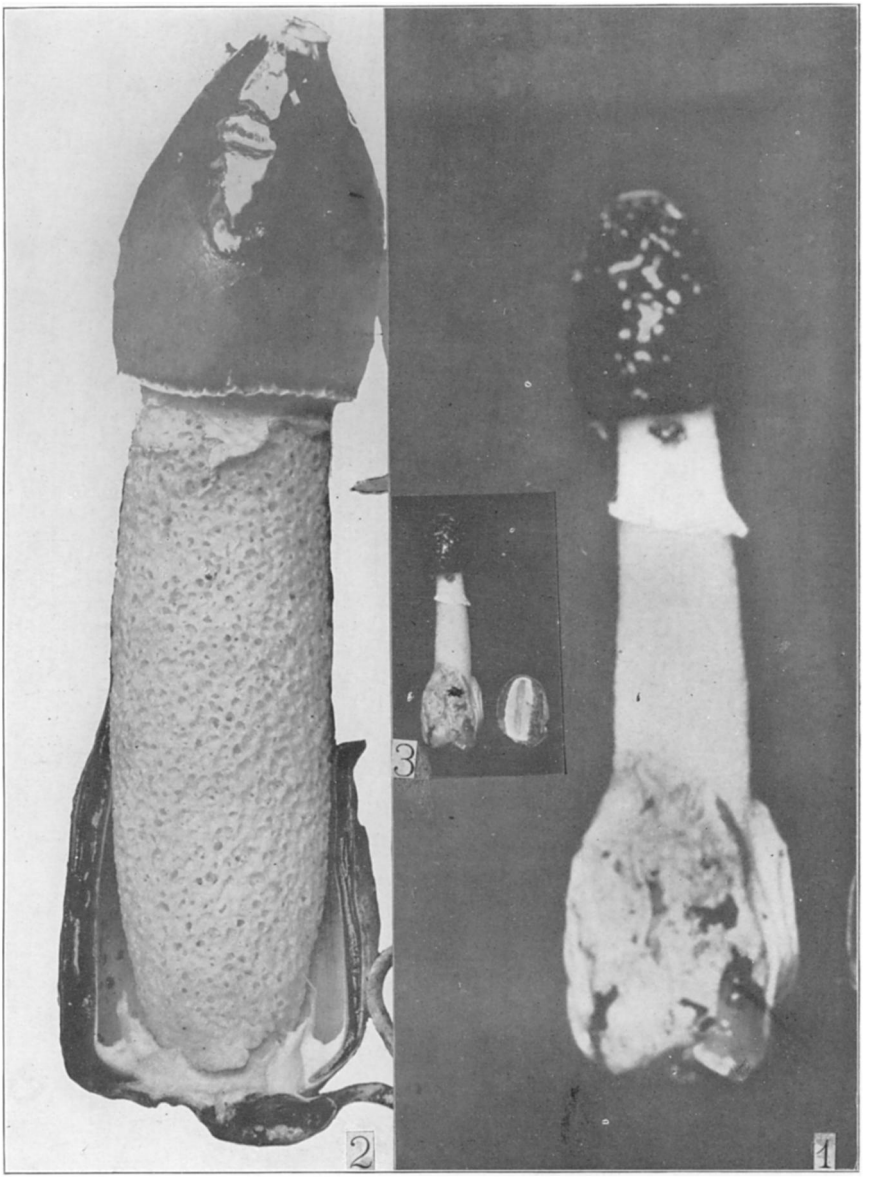
FIG. 16.—Transverse section through middle part of egg of *Dictyophora duplicata: A*, stem; *BB*, fundamental tissue lying on either side of *I* (indusium); *P*, pileus; *G*, gleba; *D*, inner peridium; *F*, gelatinous layer of volva.

PLATE VII

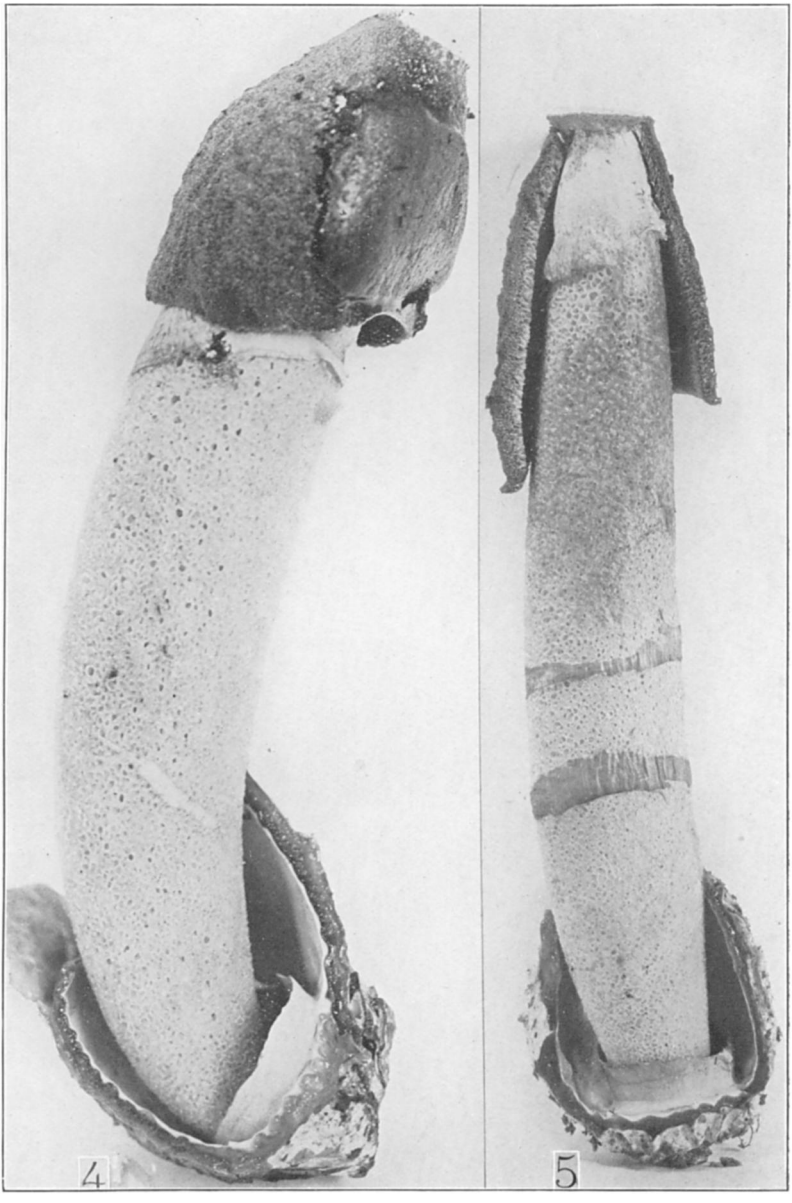
Ithyphallus impudicus from Jura Mountains, France; sections showing different stages in development of young fruit bodies.

FIG. 17.—Very young fruit body showing gelatinous area near the apex; the dark area is the fundament of the fruit body.

FIGS. 18–22.—Older stages showing early differentiation of parts of fruit body: *A*, stem; *I*, rudimentary indusium; *P*, pileus; *D*, inner peridium; *G*, gleba.



ATKINSON on DICTYOPHORA AND ITHYPHALLUS



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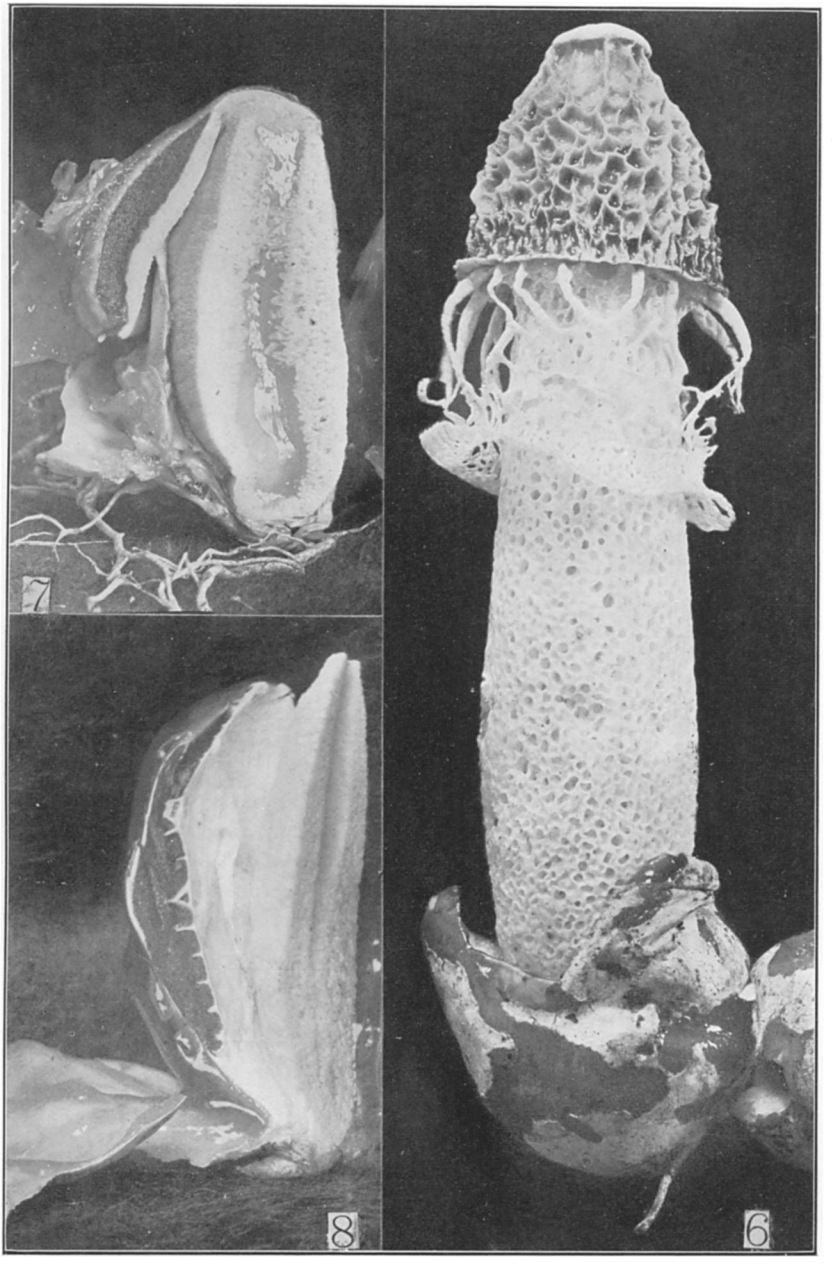

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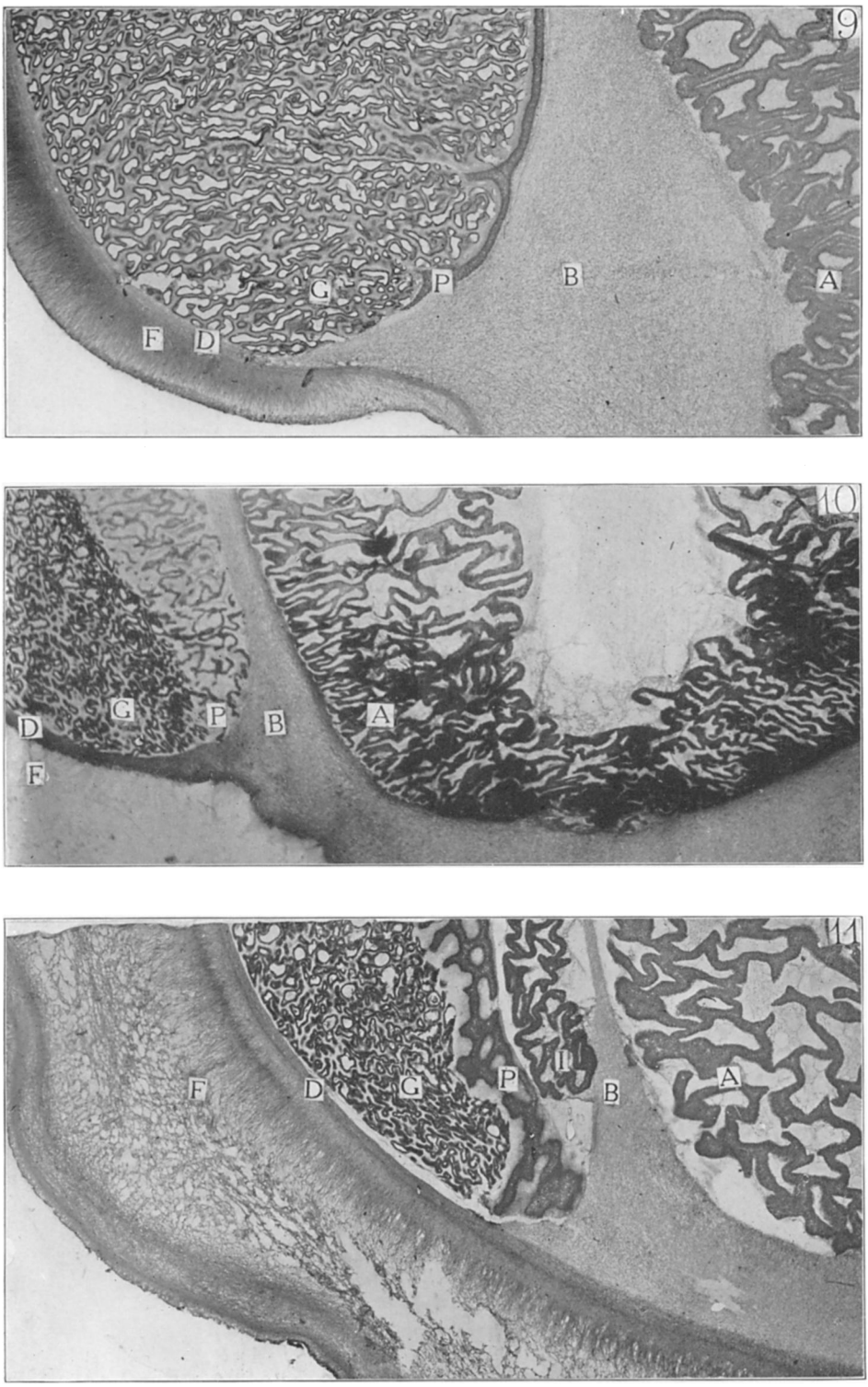

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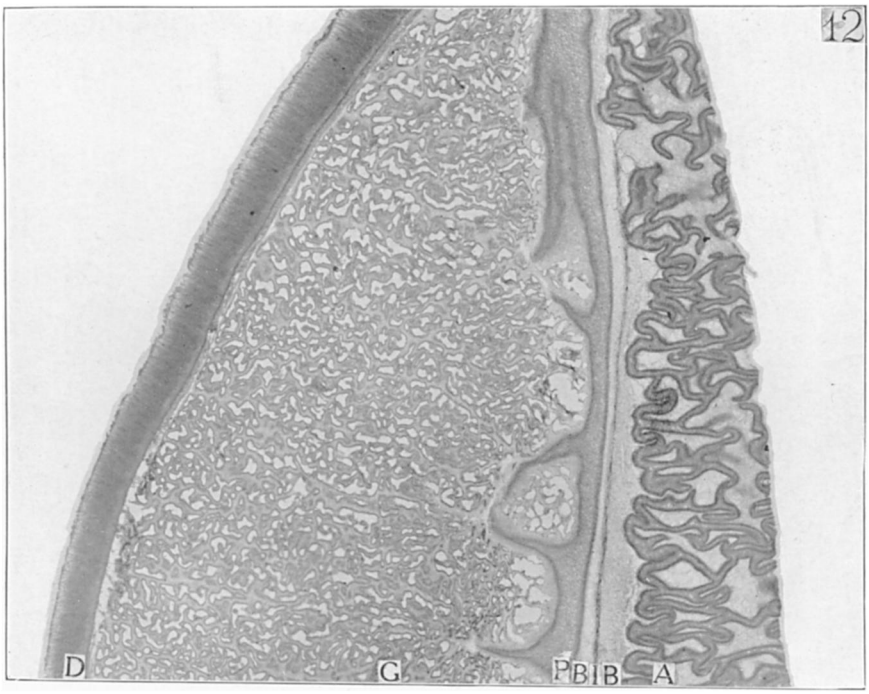

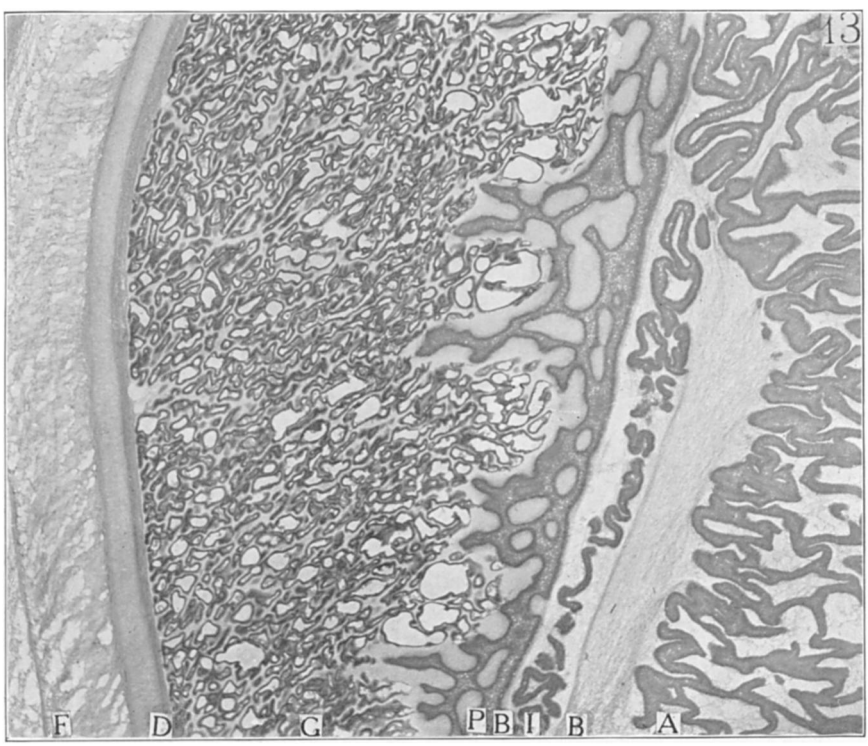

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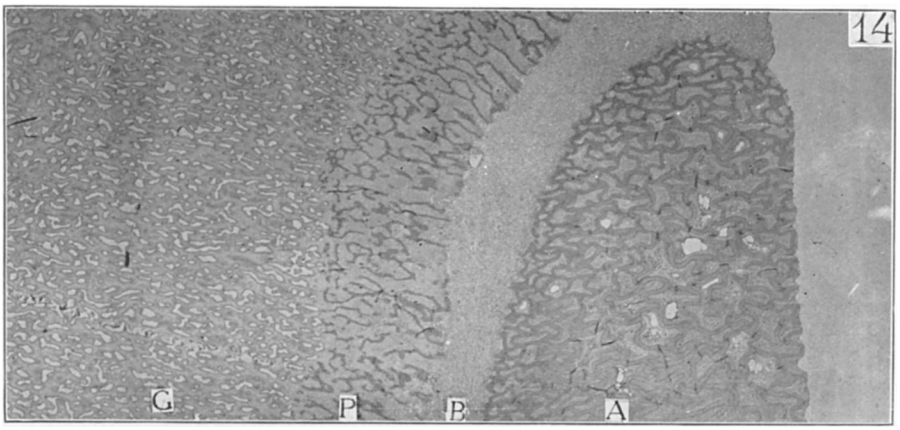

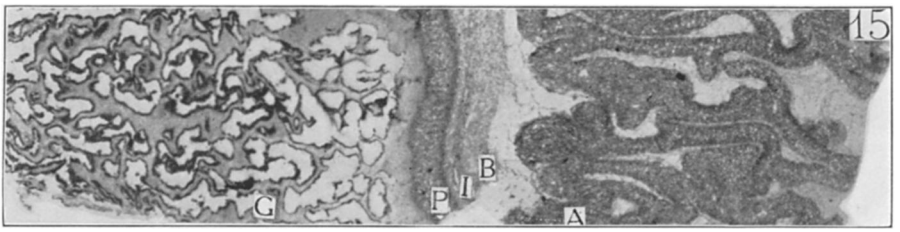

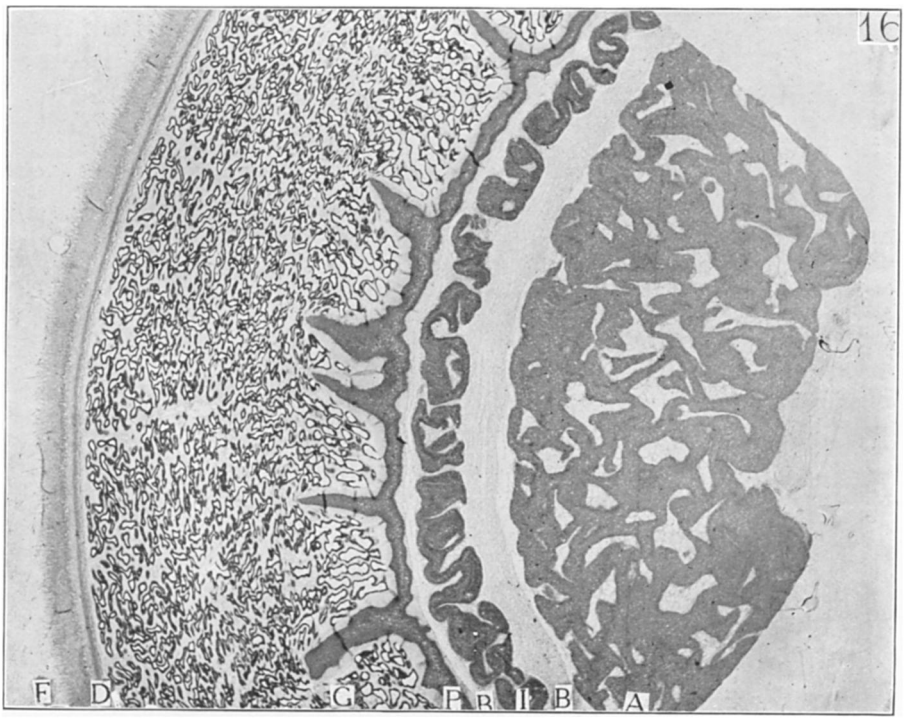

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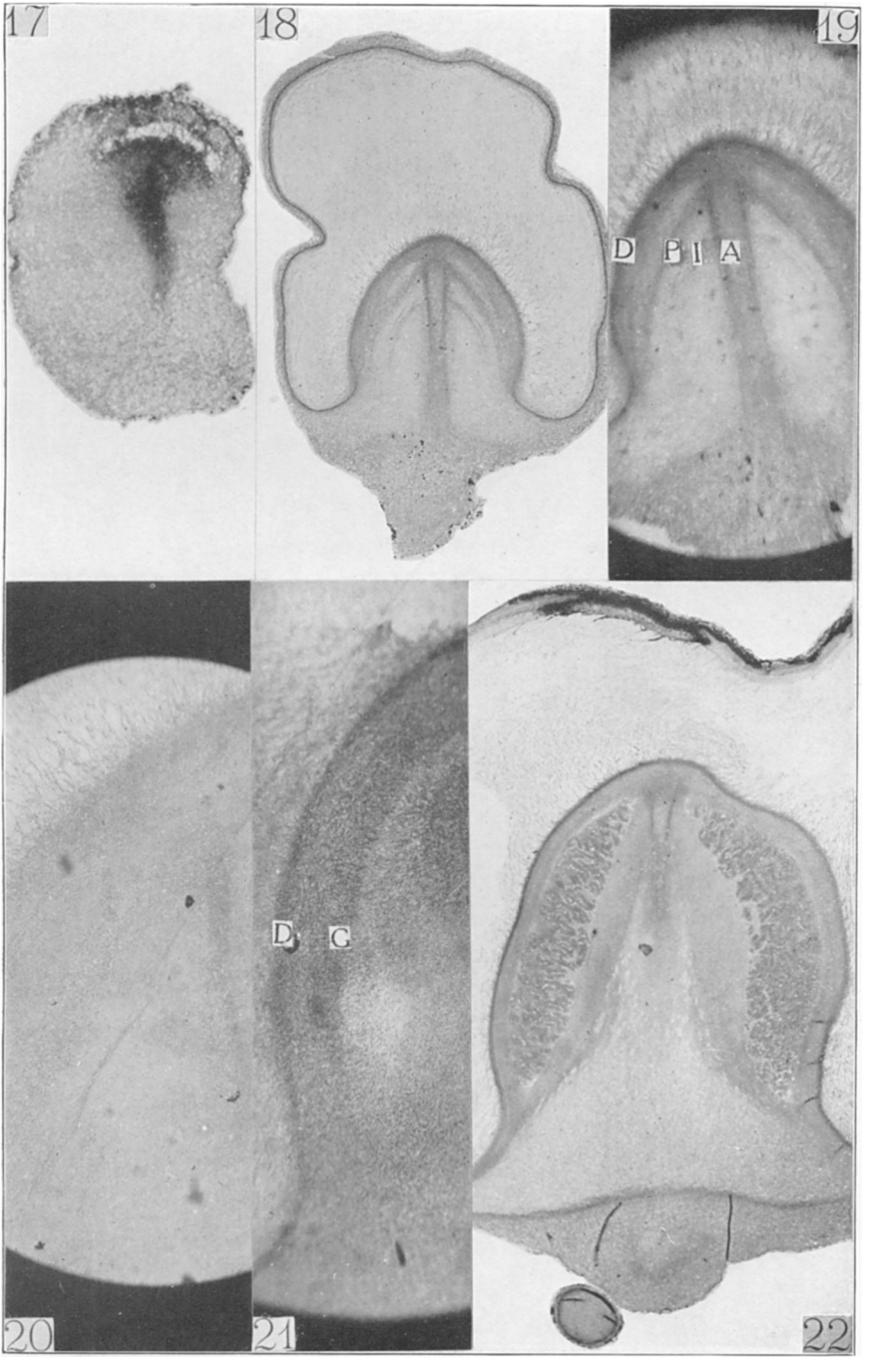

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